A new species of *Plicopurpura* (Mollusca: Rapaninae) from the Lower Miocene Cantaure Formation of Venezuela

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ABSTRACT. A new species of *Plicopurpura* (Mollusca, Gastropoda, Muricidae, Rapaninae) is described from the Lower Miocene Cantaure Formation of the Paraguaná Peninsula, Venezuela. This is the earliest record of the genus, which is represented in the Recent fauna by closely related species on either side of the Isthmus of Panama. This ancestral form still retains some characters common to most Rapaninae and has not yet developed the strongly inflated, auriculiform last whorl typical of the genus today. *Purpura weisbordi* Gibson-Smith & Gibson-Smith, 1979 is considered a junior subjective synonym of *Plicopurpura patula* (Linnaeus, 1758).

INTRODUCTION

Jung (1965) provided a systematic description of the fossil molluscan assemblage of the Cantaure shellbeds, on the Paraguaná Peninsula, Venezuela, including 95 gastropod species. A slow but steady trickle of later papers has dealt with undescribed taxa not covered in the initial monograph (Gibson-Smith 1974, 1979; Gibson-Smith & Gibson-Smith 1982, 1983, 1985; Vokes 1992, 1995; Landau 1996; Landau & Petit 1996; Gibson-Smith et al. 1997; Vermeij & Vokes 1997; Vermeij 2001, 2006; Landau et al. 2007; Vermeij et al. 2009; Beu 2010). Although these works have added another 51 gastropod species to the assemblage (see Appendix 1), there are probably about another 100 species still undescribed or unrecorded in the Cantaure fauna. In this and subsequent papers we hope to make the full extent of the gastropod assemblage of Cantaure known.

The Cantaure Formation (Hunter 1978; Gibson-Smith & Gibson-Smith 1979), with a thickness of about 75m (Jung 1965), is exposed in a series of arroyos about 500 m south of an abandoned house known as "Casa Cantaure", which is 14km west of Pueblo Nuevo in the Paraguaná Peninsula of Venezuela. The base of the unit is a *Balanus* bed containing blocks of granite, passing upwards through sands and calcareous sands (Hunter & Bartok 1974). Díaz de Gamero (1974), based on planktic forams, assigned a Lower Miocene age to the Cantaure Formation, placing it in the *Globigerinatella insueta* and *Praeorbulina glomerosa* Zones of Bolli (1966) and Zones N7-N8 of Blow (1969). Rey (1996) confirmed this age based on the nannofossil assemblage, and placing it in the *Helicosphaera ampliaperta* and *Sphenolithus heteromorphus* Zones, NN4-NN5.

The fullest understanding of the assemblage of fossil molluscs found in Cantaure is important from a taxonomic point of view; there is a high level of endemism (Jung 1965; Landau et al. 2008) and there is an important component of hard-bottom-dwelling gastropods (Vermeij 2001; Landau et al. 2009), which is very unusual in the Caribbean Neogene assemblages. It is also important from a paleobiogeographical standpoint, being chronologically the oldest Neogene deposit situated in the southernmost part of the Gatunian palaeobiogeographic province (Vermeij & Petuch 1986; Vermeij 2005; Landau et al. 2008).

Material and Methods

The material described here is from the Gibson-Smith collection housed in the Naturhistorisches Museum Basel (NHMB coll.), Switzerland and the Bernard Landau collection (BL coll.), now deposited in the Naturhistorisches Museum Wien (NHMW coll.), Vienna.

Most of the Caribbean Neogene literature distinguishes a Lower (Early), Middle and Upper (Late) Pliocene. In this series of papers on the Cantaure assemblage we have adopted the recent

recommendation of the International Commission on Stratigraphy – accepted by the IUGS on June 30, 2009 – on the redefinition of the Pleistocene (now including the Gelasian Stage/Age as its lowermost unit), and the concomitant formal redefinition of the base of the Quaternary System/Period (and thus the Neogene/Quaternary boundary) by the Monte San Nicola GSSP and thus to be coincident with the bases of the Pleistocene and Gelasian.

SYSTEMATIC PALAEONTOLOGY

The description adopts the terminology suggested by Merle (1999, 2001), in which the following abbreviations are used:

P: Primary cord
s: secondary cord
SP: Subsutural cord
P1: Shoulder cord
P2-P6: Primary cords of the convex part of the teleoconch whorl
s1-s6: secondary cords of the convex part of the teleoconch whorl
example: s1 = secondary cord between P1 and P2; s2 = secondary cord between P2 and P3, etc.

APERTURE

ID: Infrasutural denticle
D1 to D6: Abapical denticles

SUPERFAMILY MURICOIDEA Rafinesque, 1815
FAMILY MURICIDAE Rafinesque, 1815
Subfamily **RAPANINAE** Gray, 1853
Genus ***Plicopurpura*** Cossmann, 1903

Plicopurpura primitiva n. sp.
Figs 1-6

Type material and dimensions. Holotype NHMB coll. NMB H18370, height 22.3 mm (Figs 1-3); paratype NHMW 2009z0075/0002, height, 21.4 mm (Figs 4-6).

Type locality. Cantaure Formation (early Miocene: Burdigalian), lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Falcón, Venezuela (=locality GS12PGNA of Gibson-Smith & Gibson-Smith, 1979).

Diagnosis. A *Plicopurpura* species, with a small, solid shell, the last whorl has a relatively low expansion rate, thickened outer lip, denticulate within and sculpture of five broad elevated cords bearing rounded nodules.

Description. Shell small for genus, ovate, solid, with short spire, rapidly expanding whorls. Protoconch not preserved. Teleoconch of about 3.5 whorls. Suture superficial, initially straight, later undulating. Sculpture on first whorl eroded. Second whorl abraded, two nodulous spiral cords present, adapical cord at shoulder, delimiting broad, gently sloping sutural ramp; abapical cord at the suture; third nodulose spiral cord appearing on sutural ramp close to adapical suture on second half of penultimate whorl; secondary spiral thread developing between each pair of primary nodulous cords. Last whorl globose, P1-P5 broad, elevated, nodulose; SP narrower, weakly nodulous. Four secondary spiral cords of equal strength overly primary cords; s1 to s5 present with one tertiary spiral thread in interspaces on either side. Entire surface covered with close-set growth lamellae, giving somewhat scabrous appearance. Aperture wide, ovate, outer lip bevelled, crenulated in conformity with primary spiral cords; denticulate within, denticles just within lip margin, but not extending to it, extending into aperture as interrupted lirae; ID small, D1 strongest, D2-D5 of roughly equal strength; anal notch marked by very narrow adapical groove; siphonal canal narrow, open, slightly abaxially curved. Inner lip almost straight, weakly concave in parietal area; columellar and parietal area on venter forming a wide concavity; columellar callus thin, closely adpressed. Siphonal fasciole relatively prominent, rounded; positions of previous canals marked as coarse scabrous lamellae.

Discussion. The description given above is based on both the holotype and the paratype. Vermeij & Carlson (2000, p. 25) noted that an undescribed species of *Plicopurpura* was present in the Cantaure assemblage, represented by a single specimen in the Gibson-Smith collection in Basel, somewhat eroded and missing its spire (holotype, Figs 1-3). A second specimen was found by us (BL, 2005) with an incomplete aperture, but with well preserved surface sculpture and spire eroded, but present. Attempts to find further specimens during subsequent visits have been unsuccessful.
In the Recent fauna, closely similar species occur on either side of the Isthmus of Panama, *Plicopurpura patula* (Linnaeus, 1758) in the Caribbean Province and *Plicopurpura columellaris* (Gould, 1853) and *P. pansa* (Lamarck, 1816) in the Eastern Pacific Province. The Pacific forms have lower expansion rates than the Caribbean ones, giving the shell a less auriculiform shape, the tubercles on the spiral cords are finer and there are denticles often present within the aperture. Keen (1971) recognised both species in the tropical eastern Pacific, *P. columellaris* and *P. pansa,* and suggested they could easily be separated by the size of their shells and the colour of their apertures. Wellington & Kuris (1983) considered these two taxa to be conspecific. Kool (1993) discussed the presence of two *Plicopurpura* species, one on either side of the Isthmus of Panama, which he considered distinct taxa as the two no longer interbreed in nature. Arias-Rodriguez et al. (2007)

again separated the two tropical eastern Pacific species on the basis of chromosome analysis. Domínguez-Ojeda et al. (2009), based on laboratory observations on the reproduction and development of the two species, noted there were changes in their morphology at different reproductive stages in their embryonic and larval development and in the process of regeneration of their copulative organ. They again suggested the two tropical eastern Pacific "species" might be subspecies or morphological variation due to environmental conditions. Based on shell characteristics present in the large Recent Tropical American Pacific collections available to us (GJV), both of the eastern Pacific morphotypes are present with intergrading forms, suggesting a single species. Regardless of their degree of divergence, the Recent *Plicopurpura* shells on either side of the Isthmus of Panama are extremely similar, sharing the same inflated auriculiform last whorl, large aperture and seven or eight indistinct spiral cords bearing pointed nodules.

Plicopurpura primitiva n. sp. is clearly different from *P. patula* and *P. columellaris* in having a much smaller shell, the expansion rate of the adult teleoconch whorl is far less, resulting in a globose last whorl, rather than an auriculiform one as in the two Recent species. As a consequence of the lesser expansion rate of the last whorl in the fossil species the aperture is relatively narrower. The Recent Pacific forms of the *columellaris*-morphotype also have a less expanded last whorl than the Caribbean *P. patula*, and juvenile *P. patula* and some of the adult southern Caribbean forms also have a less auriculiform last whorl (GJV personal observation), however, in most of these Recent forms the last whorl is more expanded than in *P. primitiva*. Some shells of the *columellaris*-morphotype are the exception, which have a similarly globose last whorl and narrower aperture as seen in the fossil species. The spiral sculpture consists of fewer primary spiral cords, five as opposed to seven to eight in the living taxa, and the cords are elevated, bearing prominent nodules, as opposed to the relatively subdued cords bearing sharp nodules in the Recent shells. In some of the shells of the Recent Pacific *columellaris*-morphotype the nodules are obsolete on the last whorl, but the number of cords is always greater than in the fossil species. The inner lip is far more thickened in *P. primitiva* than in the living Caribbean *P. patula*, which tend to have a relatively thin outer lip for rapanines, and most specimens of *P. patula* do not have such prominent denticles developed within the lip as seen in the fossil species. The Recent Pacific forms of the *columellaris*-morphotype also have a less expanded last whorl than the Caribbean *P. patula*, and juvenile *P. patula* and some of the adult southern Caribbean forms also have a less auriculiform last whorl (GJV personal observation), however, in most of these Recent forms the last whorl is more expanded than in *P. primitiva*. Some shells of the *columellaris*-morphotype are the exception, which have a similarly globose last whorl and narrower aperture as seen in the fossil species. The spiral sculpture consists of fewer primary spiral cords, five as opposed to seven to eight in the living taxa, and the cords are elevated bearing prominent nodules as opposed to the relatively subdued cords bearing sharp nodules in the Recent shells. In some of the shells of the Recent Pacific *columellaris*-morphotype the nodules are obsolete on the last whorl, but the number of cords is always greater than in the fossil species. The inner lip is far more thickened in *P. primitiva* than in the living Caribbean *P. patula*, which tend to have a relatively thin outer lip for rapanines, and most specimens of *P. patula* do not have such prominent denticles developed within the lip as seen in the fossil species. The Recent Pacific forms of the *columellaris*-morphotype also have a less expanded last whorl than the Caribbean *P. patula*, and juvenile *P. patula* and some of the adult southern Caribbean forms also have a less auriculiform last whorl (GJV personal observation), however, in most of these Recent forms the last whorl is more expanded than in *P. primitiva*. Some shells of the *columellaris*-morphotype are the exception, which have a similarly globose last whorl and narrower aperture as seen in the fossil species. The spiral sculpture consists of fewer primary spiral cords, five as opposed to seven to eight in the living taxa, and the cords are elevated bearing prominent nodules as opposed to the relatively subdued cords bearing sharp nodules in the Recent shells. In some of the shells of the Recent Pacific *columellaris*-morphotype the nodules are obsolete on the last whorl, but the number of cords is always greater than in the fossil species. The inner lip is far more thickened in *P. primitiva* than in the living Caribbean *P. patula*, which tend to have a relatively thin outer lip for rapanines, and most specimens of *P. patula* do not have such prominent denticles developed within the lip as seen in the fossil species. The Recent Pacific forms of the *columellaris*-morphotype also have a relatively thicker lip with denticles within as in *P. primitiva*, and some have indistinct folds on the ventral part of the columellar surface, absent in the *pansa*-morphotype, *P. patula* and the new fossil form. Unfortunately we have insufficient specimens of *P. primitiva* to have an idea of the intraspecific variability. The fossil species from Cantaure seems to be a *Plicopurpura* in the making, retaining many of the features common to other Rapaninae; a globular shape, solid shell, prominent spiral cords bearing nodules and a thickened, bevelled, outer lip bearing denticles within.

There is a sparse record for *Plicopurpura* in the fossil literature. Weisbord (1962) recorded *P. patula* from the Lower Pleistocene upper Mare Formation of Venezuela (Bermúdez & Fuenmayor, 1962; Gibson-Smith & Gibson-Smith, 1979; Macsotay, 2005b). These same specimens were later described as a new taxon *Purpura weisbordi* by Gibson-Smith & Gibson-Smith (1979) on the basis of the shape of the inner lip when viewed across the edge of the outer lip. Interestingly, one of the Holocene specimens from Amuay Bay, Paraguaná Peninsula of Venezuela (BL coll.) has the same excavation to the central part of the columella seen in the shell illustrated by Weisbord (1962, pl. 26, figs 15-16) resulting in a concave portion with a very sharp edge, slightly more rounded than the angular excavation seen in Wesibord's shell. Apart from this curious feature the shells described as *Purpura weisbordi* are indentical to *P. patula*. In our opinion this is more likely to be a pathological deformity or post mortem changes than a morphological feature. For example, shells occupied by the terrestrial hermit crab genus *Coenobita*, have part of the columella missing (Ball, 1972, Kinosita & Okijama, 1968; Vermeij, 1987). We therefore consider *Purpura weisbordi* by Gibson-Smith & Gibson-Smith, 1979 a junior subjective synonym of *P. patula*. Aguilar & Fischer (1986) listed *P. pansa* for the Upper Pleistocene Montezuma Formation of Pacific Costa Rica (Baumgartner et al., 1984). We (BL) have specimens of *P. patula* from the Upper Pleistocene and Holocene of Venezuela, but as far as we are aware this is the first pre-Pleistocene record for the genus.

There is no information on where the holotype was found in the Cantaure beds. However, the paratype was found in the "lower bed" of Gibson-Smith & Gibson-Smith (1979), a bed of coarser sand lying on a *Balanus* bed containing blocks of granite (Hunter & Bartok 1974). Most of the rapanine gastropods present in the Cantaure assemblage are found in this lower unit (see Vermeij 2001; personal observation BL). This is to be expected, as *Plicopurpura* is an intertidal genus associated with rocky shores and in the Cantaure assemblage several other taxa associated with hard bottoms are found more commonly or almost exclusively in the "lower bed" (*Nerita*, undescribed *Tegula*, *Stramonita*, *Thais*, *Neorapana*, *Microrhytis*, *Ocinebrina*, *Hesperisternia*, *Macron*, and a large undescribed limpet; see Vermeij et al. 2009; personal observation BL). This assemblage of hard-bottom-dwelling gastropods found in the "lower bed" in Cantaure is extremely important as it is unparalleled in the rest of the tropical American Neogene and gives a glimpse into the taxa that inhabited these environments in the southern Gatunian Province at the beginning of Neogene time.

Etymology. The name reflects this being the earliest known *Plicopurpura* species.

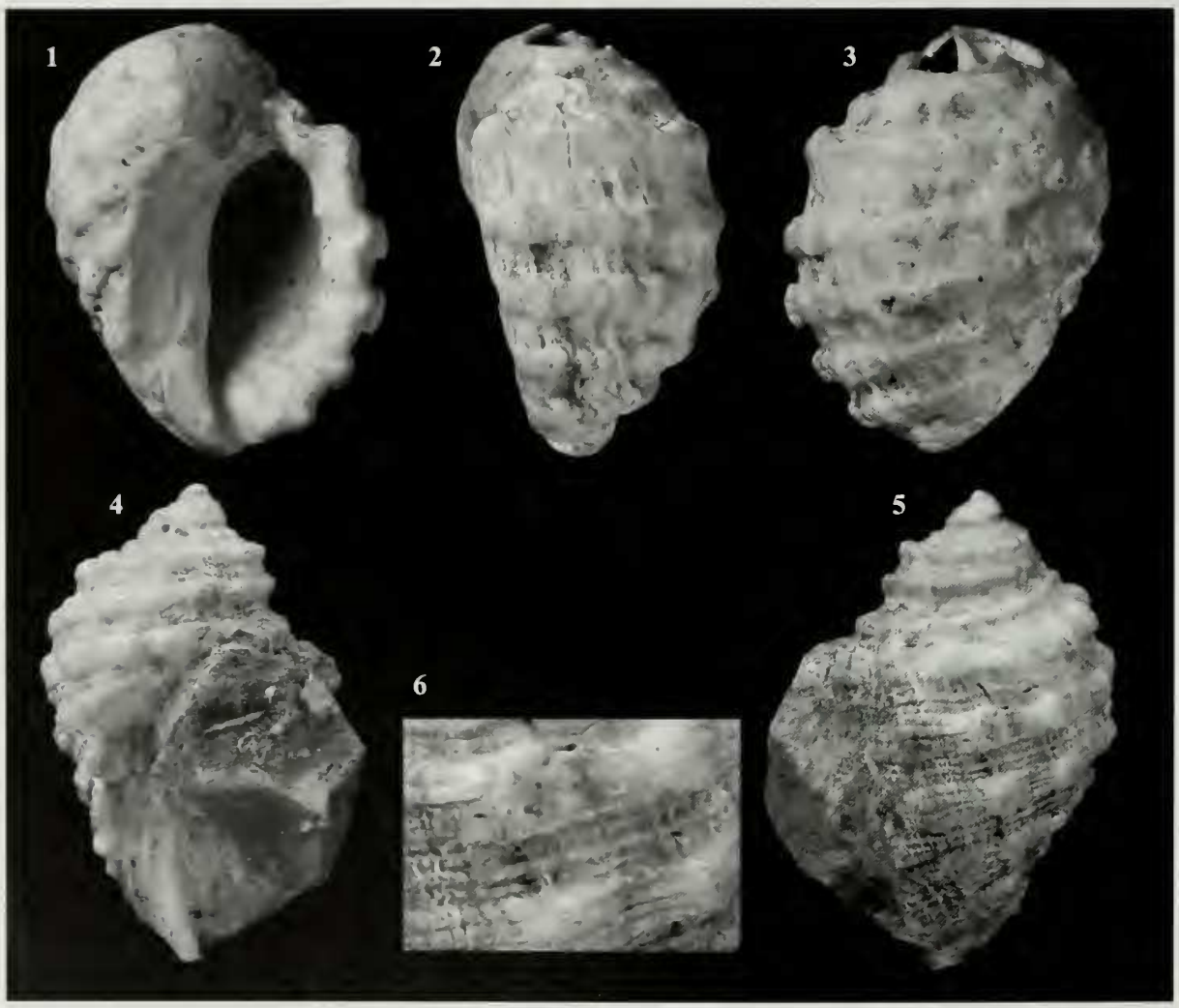

FIGURE CAPTIONS

Figs 1-6 - *Plicopurpura primitiva* n. sp., Cantaure Formation (early Miocene: Burdigalian), lower shell bed, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; 1-3, holotype NMB H18370, height 22.3 mm; 4-6 - paratype NHMW 2009z0075/0002, height 21.4 mm; 6, detail of surface sculpture of last whorl.

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Appendix 1

Gastropod taxa described or recorded and figured for the Cantaure Formation of Venezuela since Jung (1965) given in chronological order of publication, with pagination and figure information when the figured specimens are from the Cantaure assemblage.

Taxon and author	Record other than original description	Page	Figure
Chicoreus (Siratus) denegatus (Jung, 1966) n.n. pro *Murex triangularis* Jung, 1965 non Brown, 1818	fig. in Jung, 1965	77	pl. 70, figs 1-2
Voluta cantaurana Gibson-Smith, 1973		68	pl. 3, figs 1-3
Mitrella cantaurana (Gibson-Smith & Gibson-Smith, 1974) (originally described as *Strombina*; see Jung, 1989)		58	pl. 2, fig. 8, pl. 3, fig. 8, pl. 4, figs 8-10
Simnia winifredae Gibson Smith, 1974		88	pl. 1, figs 1-2
Jenneria venezuelana Gibson-Smith, 1974		92	pl. 1, figs 8, 10, 11, 12
Vasum tuberculatum Gabb, 1873	E. Vokes, 1979, 1998	112	pl. 2, fig. 3
Harpa myrmia Olsson 1931	Gibson-Smith & Gibson-Smith, 1982a	57	figs 1-3
Tralia venezuelana Gibson-Smith & Gibson-Smith, 1982b		119	figs 7-9
Melongena venezuelana Gibson-Smith & Gibson-Smith, 1983		720	figs 1-5, 13
Torquifer barbascoana Gibson-Smith & Gibson-Smith, 1983		727	figs 8-9
Pedipes mirandus Gibson-Smith & Gibson-Smith, 1985		88	fig.1
Endolium subfasciatum Sacco, 1890	Gibson-Smith & Gibson-Smith, 1989	119	fig. 1
Chicoreus cornurectus (Guppy, 1876)	E. Vokes, 1989	31	no fig.
Chicoreus corrigendum E. Vokes, 1989		34	no fig.
Sincola (Dorsina) pigea (Olsson, 1964)?	Jung, 1989	251	no fig.
Poirieria (Panamurex) improcerus E.Vokes, 1992		46	pl. 9, figs 5-6
Poirieria (Panamurex) gibsonsmithi E.Vokes, 1992		48	pl. 10, figs 5-6
Muricopsis (Risomurex) crassicosta (Benoist, 1873)	E. Vokes, 1994	72	no fig.
Chicoreus winifredae E.Vokes, 1995		119	pl. 1, fig. 1
Morum (Oniscidia) jungi Landau, 1996		53	pl. 1, figs 1-2
Cancellaria hodsonae Landau & Petit, 1997	fig. in Jung, 1965	145	pl. 75, figs 7-8
Cancellaria (Bivetiella) jungi Landau & Petit, 1997	fig. in Jung, 1965	146	pl. 75, figs 1-2
Cancellaria (Charcolleria) emilyvokesae Landau & Petit, 1997		147	pl. 1, fig. 1
Cancellaria (Massyla) cantaurana Landau & Petit, 1997		147	pl. 1, fig. 2
Axellela yara Landau & Petit, 1997		148	pl. 1, fig. 3
Narona barystoma (Woodring, 1970)	Landau & Petit, 1997	148	pl. 1, fig. 4
Macron constrictus G-S & G-S & Vermeij, 1997		358	figs 1-3
Neorapana rotundata G-S & G-S & Vermeij, 1997		360	figs 4-9
Ocinebrina francesae Vermeij & E. Vokes, 1997		78	pl. 2, figs 1-5
Pterorytis (Microrhytis) christopheri Vermeij & E. Vokes, 1997		101	pl. 12, figs 1-3
Thais brevicula Vermeij, 2001		697	figs 1.1-1.4
Stramonita bifida Vermeij, 2001		700	figs 1.5-1.7
Stramonita semiplicata Vermeij, 2001		701	figs 1.26-1.28
Hesperistemia distans Vermeij, 2006			
Cancellaria (Bivetiella) lugogonzalezorum Landau, Petit & Silva, 2007		33	figs 17-19
Cancellaria (Bivetopsia) herberti Landau, Petit &		35	figs 23-25

Silva, 2007			
Nerita rugulosa Vermeij, Frey & Landau, 2009		63	figs 1-3
Nerita (Theliostyla) pancigranosa Vermeij, Frey & Landau, 2009		66	figs 4-6
Bursa rhodostoma (G. B. Sowerby II, 1835)	Beu, 2010	57	pl. 5, figs 10, 12
Bursa rugosa (G. B. Sowerby II, 1835)	Beu, 2010	59	pl. 6, fig. 7
Distorsio biangulata Beu, 2010		80	pl. 22, figs 4, 7; pl. 51, figs 4, 5
Distorsio jungi Beu, 2010		90	pl. 16, figs 1-11
Distorsio mcgintyi Emerson & Puffer, 1953	Beu, 2010	92	no fig.
Monoplex cercadicus (Maury, 1917)	Beu, 2010	148	no fig.
Monoplex jackwinorum Beu, 2010		155	pl. 37, figs 6-9
Monoplex ritteri Schmelz, 1989	Beu, 2010	172	pl. 43, figs 2-4
Turritriton domingensis (Gabb 1873)	Beu, 2010	193	no fig.
Cypraecassis cantamrana Beu, 2010		225	pl. 63, figs 3-7; pl. 64, figs 4, 9
Cypraecassis testiculus (Linnaeus, 1758)	Beu, 2010	228	no fig.
Echinophoria hadra (Woodring & Olsson 1957)	Beu, 2010	243	no fig.
Semicassis aldrichi (Dall 1890)	Beu, 2010	246	pl. 68, figs 6, 8